

***Pteris* × *delchampsii*, a Spontaneous Fern Hybrid from Southern Florida**

W. H. WAGNER, JR.* and CLIFTON E. NAUMAN**

The genus *Pteris* comprises over 200 tropical and subtropical species, and hybridization among its species is well known. Many of the species-groups, such as the *P. longifolia* and *quadriaurita* groups, include both Old World and New World endemics. The Chinese Ladder Brake, *P. vittata* L., which is a member of the *P. longifolia* group, has been introduced into the Americas, where it frequently grows with or near closely related native species. For instance, Maxon (1926, p. 436) wrote that *P. vittata* "has escaped from cultivation and become well established in St. Thomas, Bermuda, Dominica, Martinique, Barbados, Trinidad, eastern Brasil, Florida, Alabama, and Louisiana." It is with the Florida occurrences that we are concerned here.

This study began when C. E. Delchamps discovered some unusual brakes growing along the Coral Gables Canal in Miami in the late 1950's. He sent examples to Wagner, who found them to be intermediate between the Chinese Ladder Brake and the Bahama Ladder Brake, *P. bahamensis* (Agardh) Fée. In April 1966, Delchamps and Wagner visited the locality and found the two species and the intermediate growing together. The intermediate, which we have found to have abortive spores, as would be expected in an interspecific hybrid, was surprisingly common at this locality. It is of special interest because it is a hybrid between a naturalized exotic species and an endemic species, which were brought together through man's activities. Recently Nauman made special searches for these plants in southern Florida and discovered several new localities for the hybrid, which is herewith described.

***Pteris* × *delchampsii* W. H. Wagner & C. E. Nauman, hybr. nov.**

Inter *P. bahamensem* et *P. vittatam* intermedia, sporis abortivis; squamae rhizomatis atrogriseae; squamae petioli pallido-brunneae; pinnae mediae frondis fertilis matura (3)4(5) mm latae, remotae, 1.2–1.8 cm distantes; circumferentia pinnae ab imo ad summum gradatim decrescens; segmentum sterile margine denticulatum; coenosori maturi usque ad 1–2 mm a costa extensi.

TYPE: North bank of the Coral Gables Canal at 61st Ave. and Waterway Drive, Miami, Dade County, Florida, 17 April 1966, W. H. Wagner 66013 & C. E. Delchamps (MICH).

PARATYPES (All Dade County, Florida): Coral Gables Canal bank, SW 39th St. near 62nd Ave., *Delchamps* in 1960 (MICH); Ca. 30 ft from N bank of the Mowry Canal (C-103) at junction with Tennessee Road, plants in full sun, ca. 10 individuals, 28 June 1979, C. E. Nauman & D. F. Austin 738 (MICH), 739 (FAU); Nixon-Lewis Hammock, W end of Avocado Road, 27 Feb 1979, Nauman et al. 652 (FAU, MICH); Sweetwater, open field near 122 SW 127th Ave., 8 April 1979, T. M. Thurmond 4b (FAU, MICH); Fairchild Tropical Garden, Limestone Wall on SE side of Glade Lake, 22 Dec 1981, Nauman 1490 A-D (MICH).

*Department of Botany, University of Michigan, Ann Arbor, MI 48109.

**Department of Botany, University of Tennessee, Knoxville, TN 37916.

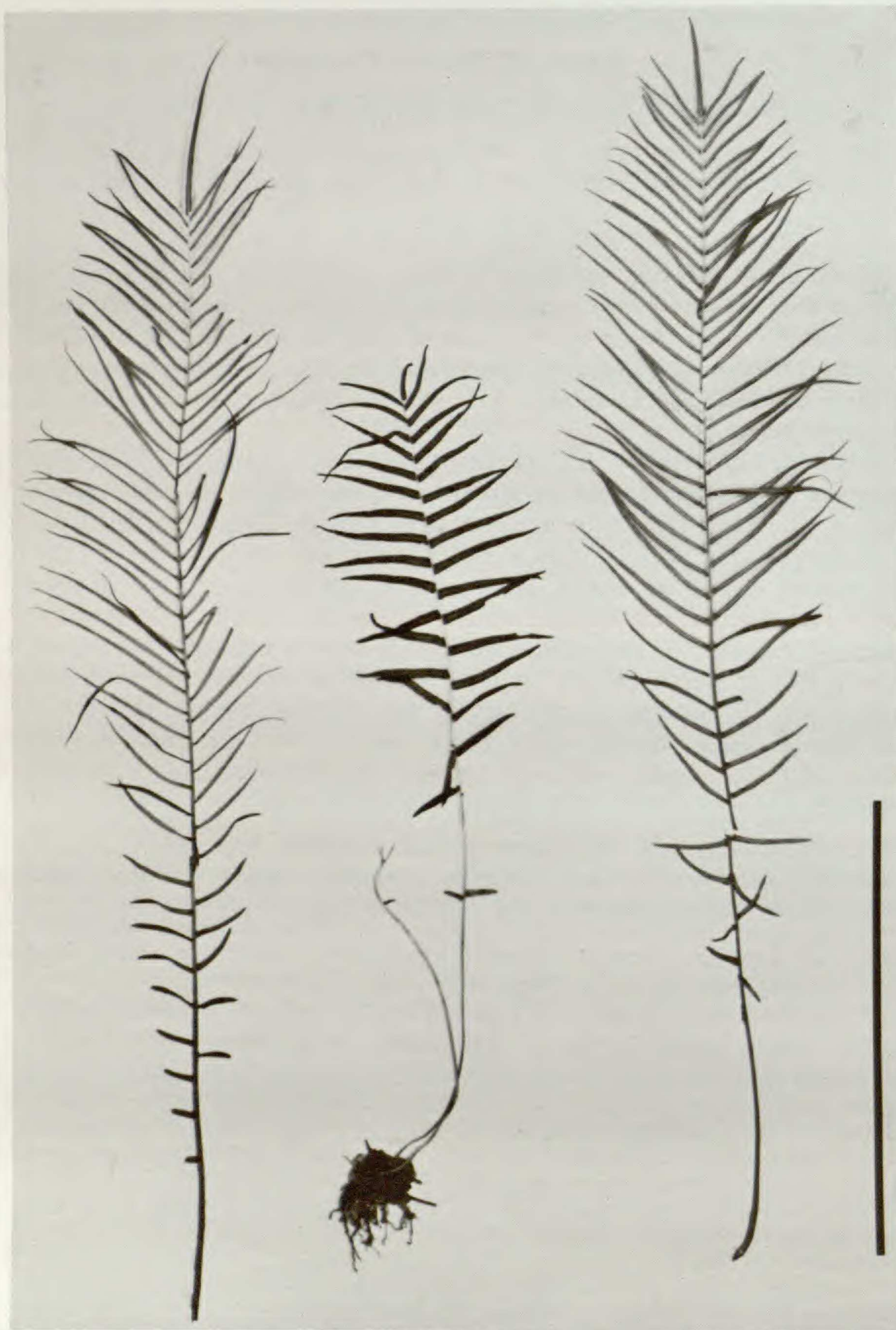


FIG. 1. Specimens from the type collection of *Pteris* \times *delchampsii* along the Coral Gables Canal, Miami, FL. Middle: Rhizome with sterile frond. Scale = 30 cm.

We name this fern for the late Dr. C. E. Delchamps, warm friend and field companion over many years, who took time out from his career as Chemistry Professor at University of Miami to explore southern Florida for rare and interesting pteridophytes. His guidance in the natural areas of Florida aided numerous researchers in their studies of problematic ferns. (See also the obituary by Mrs. C. E. Delchamps, 1978.)

At first sight, *P. × delchampsii* resembles a narrow, somewhat skeletonized *P. vittata*. However, the rhizome scales are less conspicuous, shorter (2-3 mm long), and dark brown. The scales along the petiole are fewer than in *P. vittata*, but they do have the latter's pale tan color. The pinnae are more stiff, remote, and considerably narrower. The apical pinnae are less ascending, and the sterile pinna margins (wholly sterile pinnae, and tips of partially fertile pinnae) are not so coarsely or so sharply dentate as in *P. vittata*. The coenosori of *P. × delchampsii* do not expand so much as do those of *P. vittata* when the sporangia have matured and discharged, probably due in part to abortion of the spores and failure of many sporangia to open, but the coenosori of the hybrid nevertheless come closer to the costa than do those of *P. vittata*.

Hybrids found in open, disturbed areas in full sun more closely resemble *P. bahamensis* in their stiffly erect habit and slightly revolute pinnae. Under shaded conditions, the fronds are more lax and arching and the pinnae are not revolute, and so closely resemble those of *P. vittata*.

Specimens suspected of being *P. × delchampsii* can be confirmed as that by observing the extensively aborted spores, which are unlike the normal, uniform spores of the parents. A diagnostic key to the parents is given below as an additional aid in separating the hybrid from its parents and the parents from one another, as well as in detecting backcrosses. The key is based upon our Florida collections.

KEY TO THE PARENTS OF PTERIS × DELCHAMPSII

1. Fronds stiff and nearly upright; rachises glabrous, shiny, wiry; rhizome scales relatively inconspicuous, dark brown to blackish, 1-2 mm long; stipes scaly only at the base; pinnae thick, leathery, 5-8 pinna widths distant, linear, round at the apex, the apical ones usually spreading, not strongly ascending, the sterile margins subentire to entire, lacking pointed teeth; middle fertile pinnae narrow, usually (2)3(4) mm wide; mature coenosori nearly touching the costa, thus exposing little lamina surface; old fronds persisting as naked rachises, the pinnae having disarticulated. *P. bahamensis*
1. Fronds rather lax and spreading; rachises with more or less numerous, conspicuous, narrow, pale tan scales or fibrils; rhizome scales densely tufted, pale tan, 2-4 mm long; stipes scaly throughout; pinnae thin, chartaceous, 0.5-2 pinna widths distant, linear-lanceolate, narrowly pointed at the apex, the apical ones usually strongly ascending, the sterile margins coarsely and sharply toothed; middle fertile pinnae usually (4)6(9) mm wide; mature coenosori separated from the costa 1-3 mm, thus exposing much lamina surface; old fronds simply drying up and turning brown, the pinnae not disarticulating.....*P. vittata*

Pteris bahamensis occurs in Broward, Collier, Dade, and Monroe counties in southern Florida. Outside of the United States, the species has been reported in the Bahamas, Cayman Islands and Cuba (Maxon, 1926, p. 433; Proctor, 1977, p. 141). In Florida, *P. bahamensis* occurs but infrequently in disturbed areas, and then only in or adjacent to pinelands. Typically it frequents rocky pinelands, growing in

crevices of oolitic limestone, usually rooted in circumneutral to slightly acid marl and in pockets of humus. The canopy of these habitats is composed of Slash Pine, *Pinus elliottii*. The shrub layer varies in its dominant species but typically contains *Serenoa repens*, *Coccothrinax argentata*, *Metopium toxiferum*, *Guettarda scabra*, and a variety of other species. The herb layer is dominated by assorted grasses, of which *Schizachyrium rhizomatum* is a conspicuous example.

Plants of *P. bahamensis* may attain a height of over one meter in this habitat. Older specimens often have litter a decimeter or more deep at their bases composed of old fronds, pine leaves and other debris. Fires in these areas frequently destroy plants completely, but recolonization evidently occurs quickly, and within a period of a few months new plants appear.

The Chinese Ladder Brake, *P. vittata*, occurs scattered throughout Florida and other parts of the southeastern United States at least as far north as the Carolinas and as far west as Louisiana. The plants are frequent in disturbed locations on calcareous substrates, often on limestone ledges, walls, and sinks. The plants are generally more abundant and luxuriant (up to 1 m tall) in areas of high humidity, such as canal banks and limestone sinks with standing water. In dry places, the plants are sparser and dwarfed (usually less than 0.5 m tall).

The introduced species can be found together with its native relative in pinelands, particularly around small sinkholes. However, *P. vittata* is not common in these habitats. Conversely, the ledges and walls favored by *P. vittata* are seldom inhabited by *P. bahamensis*. Hybrids have not been found in the pineland habitats, but only in adjacent areas. The type locality in southwest Miami is a canal bank in an urban, residential area. The rocky sides of the canal had numerous weeds in addition to the brakes. The other ferns were: *Anemia adiantifolia* (Wagner 66010, MICH), *Sphenomeris clavata* (66011), and *Thelypteris cf. augescens* (66009). The canal bank had been widened and most of the ferns, including the parent and hybrid Ladder Brakes, had been destroyed when Nauman visited the locality in 1977. However, he found four new sites for the hybrid during the past five years. Three plants of *P. ×delchampsii* were found along a fringe of the Nixon-Lewis hammock in a border of *Schinus terebinthifolius*. The Glade Lake population at Fairchild Tropical Garden consisted of 11 plants. Two were terrestrial in a muddy substrate on the south bank of the lake; the remaining plants were confined to a small colony about 1.5 m in diameter on the westernmost portion of a rock wall. *Pteris bahamensis* was abundant on the north face of the wall, an atypical habitat for this species. *Pteris vittata* was also abundant near the site, but there were only three small, sterile plants within 50 m of the hybrid plants. The other sites (see specimen citations) were similar in being disturbed, open areas having loose, calcareous substrates covering oolitic limestone.

The presently known range of the hybrid in Florida is in Dade County from south Miami to Homestead. We predict that *P. ×delchampsii* may be discovered in Monroe and Collier counties. Because the habitat that the hybrid prefers is becoming more common in all of these counties, we expect that its range will increase in the future, although the available natural habitat of *P. bahamensis* is disappearing. Unless the hybrids develop some means of reproduction, the fate of *P.*

\times *delchampsii* in years to come depends upon the success of *P. bahamensis* in surviving man-made changes. In all likelihood, the weedy *P. vittata* will be the ultimate survivor.

BIOSYSTEMATICS OF PTERIS \times DELCHAMPSII

It is possible that *P. \times delchampsii* may develop a means of reproducing itself, in spite of its abortive spores. (The hybrid spores display all sorts of irregularities in size, shape, and exine development, and were illustrated by DeBenedictus, 1969, pl. 26.) Commonly the number of spores or spore-like bodies per sporangium in *P. \times delchampsii* is less than 64 because normal meiosis is interrupted and a number of large, presumably unreduced spores are formed, in addition to many tiny, aborted spores. The giant spores are evidently viable, as described below.

Both the hybrid and its parents are tetraploid with $4x = 116$; the base number of *Pteris* is 29. In her studies of this plant, DeBenedictus was unable to obtain a precise count of *P. bahamensis*, but her evidence supported the conclusion that it is a tetraploid. It is interesting to note that *P. longifolia* L., of which *P. bahamensis* may be only a geographical variety, is reported by Walker (1966) also to have $4x = 116$, a number evidently characteristic of the Ladder Brake group. Unlike its sexual parents, *P. \times delchampsii* shows peculiar pairing behavior. Counts by W. H. Wagner, Jr., K. L. Chen, and V. M. DeBenedictus (vouchers in MICH) show ca. 32–35 bivalents, with the remaining chromosomes univalents.

DeBenedictus grew spores of *P. \times delchampsii* because of the possibility that it possessed a low-level expression of apogamy which enabled it to produce gametophytes that could proliferate directly into sporophytes. Such a mechanism would allow it to reproduce in its habitats. She found that gametophyte production from hybrid spores was much lower than in the parents. However, those gametophytes that did form bore many antheridia and archegonia on an especially well developed cushion region. Some gametophytes also produced peculiar growths of tissue on the wings. A few of the hybrid gametophytes became filamentous.

After flooding her cultures of *P. \times delchampsii* with water, DeBenedictus observed a few sporophytes developing. These arose from archegonia and appeared to be sexual in origin. Unlike *P. \times delchampsii*, the hybrid progeny gave $6x = 174$, which DeBenedictus explained as possibly resulting from backcrossing of *P. \times delchampsii* with one of its parents that was present as a contaminant. According to her, "Sperms produced by gametophytes of the hybrid would have 116 chromosomes. Fertilization of a parental gametophyte [with 58 chromosomes] would produce a sporophyte with $2n = 174$ " (DeBenedictus, 1969, p. 70).

The phenomenon of apparent backcrossing between "sterile hybrids" and their parents in nature also has been suspected in *Asplenosorus \times ebenoides* \times *Camptosorus rhizophyllus*, *Dryopteris (goldiana \times intermedia) \times intermedia* (Wagner, 1971), *Asplenium \times curtissii \times abscissum* (Morzenti, 1967), and *Polystichum (acrostichoides \times braunii) \times acrostichoides* (Morzenti, 1962). It is possible that "sterile hybrid" ferns are especially likely to produce unreduced spores because of their faulty pairing behavior, and that the gametophytes produced by the unreduced spores are especially prone to backcrossing with their parents. We

encourage field workers in southern Florida to make special efforts to discover new populations of *P. ×delchampsii* and its parents and to examine in detail those already known in order to find both hybrids and backcrosses. Because of its vigorous growth, *P. ×delchampsii* may become an ideal research tool, both in the wild and in the laboratory.

We wish to thank Katherine Lim Chen and Virginia Morzenti DeBenedictus for their contributions to this investigation. The University of Michigan Matthaei Botanical Gardens kindly grew cultures of the hybrid plants for our research. Most of the work described here was carried out under National Science Foundation Grant GB-3366, "Evolutionary Characters and Classification of Ferns."

LITERATURE CITED

- DeBENEDICTUS, VIRGINIA M. MORZENTI. 1969. Apomixis in ferns with special reference to sterile hybrids. Ph.D. thesis, University of Michigan, Ann Arbor, MI.
- DELCHAMPS, MRS. C. E. 1978. Curtis Eugene Delchamps (1925-1977). *Amer. Fern J.* 68:6.
- MAXON, W. R. 1926. Pteridophyta of Porto Rico and the Virgin Islands. *Sci. Surv. Porto Rico Virgin Isls.* 6:373-571.
- MORZENTI, V. M. 1962. A first report on pseudomeiotic sporogenesis, a type of spore reproduction by which "sterile" ferns produce gametophytes. *Amer. Fern J.* 52:69-78.
- . 1967. *Asplenium plenum*: a fern which suggests an unusual method of species formation. *Amer. J. Bot.* 54:1061-1068.
- PROCTOR, G. R. 1977. Pteridophyta. In R. A. Howard (ed.), *Flora of the Lesser Antilles*, vol. 2. Arnold Arboretum, Jamaica Plain, MA.
- WAGNER, W. H., Jr. 1971. Evolution of Dryopteris in relation to the Appalachians. In P. C. Holt (ed.), *The Distributional History of the Southern Appalachians*. Virginia Polytechnic Inst. State Univ. Res. Div. Monogr. 2, Blacksburg, VA.
- WALKER, T. C. 1966. A cytotaxonomic survey of the pteridophytes of Jamaica. *Trans. Royal Soc. Edinburgh* 66:169-237, pl. 1-5.